Amotz Zahavi

Tales of a Swamp and Peacock Tails

On the 12th of May 2017, the scientific world lost a pioneer, a scientist extraordinaire, and nature conservator – Amotz Zahavi. Zahavi was an Israeli evolutionary biologist and Professor of Zoology at the Tel Aviv University. Zahavi combined outstanding research in evolutionary biology and animal behaviour with environmental actions. He was known in the scientific circles for his nonconformist ideas that not only stimulated scientific debates on sociobiology and signal evolution but also often provided alternative and more accurate explanations to long-standing paradoxes. Unfortunately, some of the most fundamental ideas Zahavi proposed were almost unanimously rejected by his peers only to be eventually, and almost without exception, accepted by all, including his critics. This should give some hope to the Zahavis in the making.

Zahavi also played a pivotal role as a conservationist towards saving the wilderness of Israel, an aspect that has been overshadowed by his more fundamental work. This article will try to find a balance between the two.

Early Life and Formative Years

Born on 14th August 1928 in a town called Petah Tikva (meaning 'opening of hope'), 10 km east of Tel Aviv and what was then part of Mandatory Palestine, Zahavi was a bird watcher and nature lover even in his early years. While he nurtured his love for ornithology, he wanted to study agriculture and become a farmer and settle as part of a communal settlement (Kibbutz). However, Prof. Heinrich Mendelssohn at the Biological Institute in Tel Aviv, under whose supervision he later did both his MSc and PhD persuaded him to study biology instead. He thus registered to study biochemistry at the Hebrew University of Jerusalem. In Zahavi's own words in an anniversary essay, he wrote in Animal Behaviour in 2003: "I was attracted by the great advances in cell biology and in biochemistry that took place at that time. But after spending several months cooped up in a laboratory, I could not resist the temptation to go out again into the field, looking for rare birds and watching birds display". So he went back to his first love, ornithology. He carried out his Master's thesis work on the breeding biology of the birds of Hula Swamp (1954). It is at the University that he met Avishag Kadman, a plant physiologist, who was to become his long-term academic collaborator and collaborator for life after they married in 1954.

Zahavi spent the following year at Oxford on a British Council fellowship to study animal behaviour under the would-be Nobel laureate, Nikolaas Tinbergen [1] where he spent most of his

time observing black-headed gulls. In 1960 he started a project examining the social behaviour of wintering white wagtails. He made meticulous observations on how resource distribution could drive bird behaviour to shift from being territorial to flocking. Between 1969–1970 he travelled to Edward Grey Institute, Oxford, to work with renowned ornithologist and evolutionary biologist David Lack [1]. This was a time when the group selection[1] vs individual selection debate was at a high. Under David Lack's mentorship, Zahavi was introduced to the controversy and became a staunch supporter of individual selection. He received his PhD from Tel Aviv University in 1970. Later that year, he joined Tel Aviv University as a Faculty in Zoology and remained there till he retired. It was here that he initiated his famous long-term studies on the Arabian babblers. These studies have significantly advanced our understanding of the evolution of social behaviour, cooperation, and signalling systems.

Troubled Waters

Zahavi's formative years were times of global political turmoil. In 1939, when he was barely 11 years old, World War II broke out. The Nazi holocaust and the crisis it resulted in led to large-scale migrations, and many refugees flocked to Palestine and later Israel after it was established in 1948. While Zahavi was a Sabra (Jew born on Israeli territory) the crisis did not leave any lives untouched. The rapid influx of refugees, widespread poverty, food shortage, and disease outbreak plagued societies around the world following World War II. Moreover, in 1948, the Arab-Israeli War broke out and a 20-year-old Zahavi had to serve in the military. He subsequently returned to university education and registered for a Master's degree.

The newly formed state of Israel (1948) had little time for jubilation once the war was over. Hundreds of thousands of Palestinian Arabs and Jews were expelled or fled in opposite directions. Given the geography and limited space available in Israel, some hard choices were going to be made by Israelis that pitched sustenance and environment against each other, a battle that the latter lost on many fronts. While Zahavi was studying at the University, Jewish National Fund (JNF), a non-profit organization, embarked on an ambitious project to reclaim land in order to promote agriculture and development of the newly formed nation. One of JNF's proposals was to drain the Hula Lake. It is the northern most of Israel's three important inland water bodies (Hula and Kinneret, the two freshwater lakes, and the Dead Sea, all three connected by the Jordan river) and once spread over 1200 ha. Large parts of the Hula lake valley were swamplands lined with papyrus and home to human settlements and wildlife since prehistoric times. Given its link with the Jordan river and hence access to freshwater, it was an important site with respect to the potential for increasing farmable land. Draining the

[1]Group selection refers to the idea that natural selection can act on groups of individuals, favouring one over the other leading to traits that are advantageous to the group.

swamp was no doubt a controversial proposal. Yet, when survival was in question (due to food shortage and spread of mosquito-vector-borne diseases), preservation of the environment and swamp birds were unlikely to be a matter of concern.

Thus began the ill-fated and infamous draining of the Hula swamp, an ecological and environmental disaster in the making. In 1950, Prof. Mendelssohn sent young Zahavi to study the bird communities at the swamp and himself tried to lobby to convert part of the swamp into a nature reserve. His proposal was dismissed and JNF started their controversial work towards draining the swamp in 1951, despite outcry from scientists and naturalists about its long-term ecological demerits. For Zahavi, embarking on the task set by Prof. Mendelssohn would mean delaying University (yet again), but as Prof. Alon Tal quotes in his book [2], Zahavi finally made up his mind, "To hell with school. Soon there won't be any birds left to see" and hurriedly left to study the breeding birds of Hula swamps before they were all gone.

Fighting Losing Battles

When faced with opposing and difficult choices, governments often cater to myopic, short-term gains and it falls on the shoulders of a handful to resist. Environmentalists and conservationists even today are viewed as impractical and more seriously, as an obstacle to development. Given those times, the situation was far worse, and it required courage, determination, and unadulterated passion to fight the losing battle of saving the environment when all odds were against it. The campaign to save Hula was pioneered by Prof. Mendelssohn, who was applying academic as well as political pressure and trying all means to convince JNF to at least spare some part of the Lake as a nature reserve. However, hope for the marshes was fast dwindling.

In 1953, a landmark event in Israel's environmental history occurred when Amotz Zahavi co-founded Israel's first nature protection NGO – Society for Protection of Nature (SPNI) – in Israel. The co-founders included his environmentalist friend Azaria Alon, J H Hoofien, and Prof. Mendelssohn. The formation of SPNI gave hope to those who were against the drainage project and many looked forward to a breakthrough, albeit the process of drainage had already been initiated. However, little changed, and barely a couple years into founding SPNI, as mentioned earlier, Zahavi was off to Oxford for a year. He returned back to find a poor and powerless SPNI with a feeble membership and realised that juggling his academic interest and his conservation mission could potentially be fatal to the latter. Zahavi took another radical decision – to delay his doctoral work – and left his academic position to head SPNI for the next 15 years.

Zahavi and his co-workers were in tug-of-war with JNF, often falling flat on their faces but bouncing back again. Unfortunately, by 1958, the Hula swamp and lake complex was drained

completely leaving behind an unrecognizable landscape and a devastated ecosystem. The wetlands were gone and along with it, the freshwater and the reeds that served as an important feeding station for the migratory birds. Several species endemic to the lake ecosystem were driven to extinction, including the Hula painted frog. Zahavi, as founding director of SPNI. continued to reach out to friends and citizens to save Hula. He was helped significantly by Azaria Alon (also known as SPNI's trumpet) who campaigned and lobbied for Hula alongside his teaching duties. But with little money left even with the SPNI founding members and no infrastructural support from the government, the dreams of resurrecting Hula was fast slipping out of their fingers.

Hope for Hula

Zahavi had run out of money, and in the face of chronic financial crisis, the future of SPNI looked bleak. However, in 1956, Zahavi got a research assistant position at Tel Aviv University under Prof. Mendelssohn and with that began a renewed effort to revive SPNI. Membership campaigns, political lobbying, and newspaper and radio publicity finally paid-off and JNF agreed to resurrect part (about 300 ha) of the Hula swamp by reflooding it, a promise they did not keep for a few years to come. However, with the intervention of the National Reserve Authority, the Hula restoration project finally saw the light of day, and over the following years, gradually recovered at least a part of its original glory. The Hula Nature Reserve was officially announced in 1964. Following heavy rains in 1990, a part of the Hula Valley was flooded again and it stayed that way.

In 1996, Hula Nature Reserve was declared a Ramsar Site – a wetland of international importance. Over the years, wildlife gradually returned to the ecosystem, including thousands of migratory birds and also the Hula painted frog, once declared extinct. Every year now, Israel celebrates the Hula Valley Bird Festival during the autumn migration, taking bird lovers, scientists, and tourists through the once doomed reed-covered marshes of the Hula swamp. The people of Israel and its birds owe Zahavi and other members of SPNI a great deal. His persistent efforts to fight and eventually, partially win a losing battle will give hope to many environmentalists and activists.

Bold Ideas and Major Scientific Contributions

While fighting battles for nature, Zahavi managed to keep his academic interests alive. In 1970 Zahavi kick-started the Arabian Babbler Project in collaboration with his wife Avishag. They established a world-class facility to study these birds in the wild at the Hazeva Field Station,

which was home base to them after he retired from Tel Aviv University. He managed to ring[2] and habituate many groups of babblers in his study site. This allowed him the unique opportunity to observe the birds up close, thereby facilitating behavioural studies of these social birds. The Arabian babblers are group living, cooperative breeders, i.e., non-breeding members of the group assist breeders in raising the young ones. This altruistic act of raising other individuals' young ones, interested Zahavi deeply. It is this aspect of the babbler study that eventually led him to his most influential scientific work on the evolution of signals. Zahavi was a generator of ideas, most of which were based on his elaborate observational studies on birds. Zahavi's ideas were frequently received with copious criticism/reservation (only to be verified later in many cases). In 1973 he developed the information-centre hypothesis with Peter Ward, in which they proposed that avian roosts act as information-centres where unlucky foragers stand the chance to obtain information about the location of a resource-rich patch. The importance of this radical proposition in understanding the adaptive significance of gregariousness in birds was profound. Yet, the hypothesis received little support for a long time, like many other radical ideas proposed by Zahavi. There were at least two reasons why Zahavi's ideas faced resistance from the community. First, his ideas were often ahead of their times and second, he mostly indulged in providing verbal models based on his empirical observations and never accompanied his arguments with quantitative proofs. Notwithstanding that, his ideas, just like the man himself, could not be ignored, and more often than not, were correct.

Evolution of Social Behaviour – A Case of Individual Selection

To give a little background, the times between the 1960s and 1970s saw much debate over the theories on the evolution of social behaviour from the point of view of the unit of selection. In other words, scientists differed in their opinion with respect to the level at which natural selection operates: the group, the individual or the genes. Wynne Edwards was the most vocal and prominent advocate of group selection (GS). His argument was that an organism behaves in a manner to enhance the survival of the group to which it belongs or for the good of the species. This view was subsequently rejected by evolutionary biologists (including G C Williams and Maynard Smith) in favour of individual selection. Another model of evolution of social behaviour via kin selection (KS) was proposed by W D Hamilton. The kin selection model drew much support with the persuasive arguments Hamilton made in proposing the concept of 'inclusive fitness'. What kin selection proposes is as follows: an individual can enhance its own fitness by either raising/helping its own young ones and/or by helping relatives raise their young ones to whom the focal individual is sufficiently or closely related. Zahavi, influenced by David Lack, was a firm supporter of the individual selection model of evolution of social

[2] A ring with a number/colour is placed on a foot of each bird to facilitate individual identification.

behaviour. Zahavi opined that "models of KS are in fact models of GS among kin. They are equally unstable. Although the investment and gain in GS models are not presented by gene frequencies, any investment is ultimately turned into gains or losses in fitness. Thus, because of the potential advantage to social parasites in models of KS and GS, both are equally unstable over evolutionary time". Zahavi remained for life an ardent subscriber to the view of individual selection and in fact, continued to work on it till the end of his life, as evident from the last paper he co-authored with Prof. Vidyanand Nanjundiah (the paper was published after Zahavi's death) [3].

The Handicap Principle – Honesty in Signals

Following his individual selection model and drawing from his observations on the Arabian babblers, Zahavi developed an innovative verbal model explaining the evolution of exaggerated traits or risky/costly behaviours in animals. He theorized that costly altruistic behaviour such as chick feeding in Arabian babbler by a helper or risky behaviour such as mobbing snakes act as a status symbol for the individual to increase its social prestige within the group.

To put his findings about the evolution of exaggerated traits in context, we need to go back to Darwin who regarded his theory of evolution by natural selection to be inadequate in explaining the evolution of exaggerated traits (including behaviours) such as the long ornamental tail of the peacock. He eventually proposed the theory of sexual selection [4], an advantage some individuals have in exclusive relation to reproduction, in an attempt to explain the paradox. In summary, he proposed that natural selection would act against males bearing exaggerated traits and thereby reduce their survival chances. However, if females had a preference for exaggeration in traits and were 'charmed' by it, then males bearing such traits were likely to get more mates than those males with modest traits. As a consequence, any reduction in survival of extravagant males due to their exaggerated traits would be compensated by the increased number of offspring such males would father.

In 1958 R A Fisher extended Darwin's theory by proposing an explanation for female preference for exaggerated traits via a process he termed as run-away selection [5]. He suggested, that to begin with, a slight exaggeration of a given trait (say the length of the peacock's tail) might have been an indicator of the male's survival value or quality. Thus, females who preferred males with slight exaggerations would have better quality offspring. However, if the exaggerated trait and the preference trait were both heritable, sons of such females choosing males with an exaggerated trait would have the exaggerated trait, as well as the genes for the preference trait (that would not be expressed), and daughters of such females would have the genes for the exaggerated trait (that would not be expressed) and the preference for that trait. If

there was a genetic correlation between the exaggerated trait and the preference trait, it would result in positive feedback, with females preferring more and more exaggerated versions of the trait and males evolving increasingly exaggerated traits, even if the exaggerated trait itself becomes disadvantageous in terms of natural selection (say, predation). This positive feedback loop, fed by the run-away process, is expected to stop when the cost of carrying the exaggerated trait (such as increased mortality before reproduction because of increased susceptibility to predation due to the long tail) outweighs the benefit conferred by the trait (offspring obtained due to preference of the long tail by females).

Amotz Zahavi provided a ground-breaking idea to address the seemingly paradoxical evolution of the exaggerated tail of the peacock [6], popularly referred to as Darwin's puzzle, by proposing the following:

- Signallers evolve exaggerated versions of existing traits that receivers pay attention to.

- In doing so, they improve the ability of receivers to perceive and discriminate between different variants of the signals and thereby between the signallers.

- The exaggerated signal must be costly (energetically for instance) to produce, maintain as well as display and hence may be viewed as a handicap borne by a signaller.

- This handicapping signal should also be precarious in the sense that the signal or the signalling behaviour should break down at the slightest reduction in the signaller's quality (poor quality individuals should not be able to display the signal). In this way, the exaggerated signal (or handicap) would be a reliable or honest or true indicator of the male's quality. Receivers would evolve to pay more attention to handicapping signals which would be difficult to fake or impossible to be borne by low-quality individuals. One can think of the handicap principle in terms of show-off or over indulgence as costly traits that only the rich can afford. The same would hold in the case of the gazelle that stots (jump up and down conspicuously) in the face of a predator. Only individuals who can afford to spend additional time and energy to stot and still be able to escape if actually chased by the predator will stot in order to indicate to the predator that the chase would be pointless. Such individuals, if pursued by the predator, will outrun it and live to pass on their genes, while those who do not have such energy reserves would be better off running away rather than stotting. Therefore, stotting would be an honest signal that can be used by predators to assess whether a prey is worth chasing or not. In fact, individuals

that stot are usually ignored by predators. An earlier article in *Resonance* has discussed the handicap principle in detail [7].

As Zahavi's proposition was verbal and did not include a mathematical model or quantitative proof, the handicap principle set-off a raging debate amongst biologists, theoreticians, naturalists, and experimentalists alike. For years, it received widespread criticism, resistance and even outright rejections from evolutionary biologists. Zahavi, of course, was unperturbed and continued to work towards gathering empirical evidence for his theory and left the rest to catch up. It was only with the mathematical model proposed by Alan Grafen, elucidating how the handicap principle could work that Zahavi's contribution was gradually recognized and accepted. In later years, the handicap principle and its remarkable potential in understanding signal evolution in both human and non-human systems was penned down by the Zahavi couple in the form of a book appropriately called *The Handicap Principle – A Missing Piece of Darwin's Puzzle* which was translated from Hebrew by their daughter and son-in-law [8]. The book is written lucidly and makes a wonderful read for an expert and a curious beginner alike. That was Zahavi's style anyway. He believed in articulating his points verbally and never bothered with formalizing his ideas and packaging it in shiny wrappers of mathematical models. This was an aspect of his style of work that cost him recognition, especially for his most influential contribution – the handicap principle. Nonetheless, Grafen himself noted that "These verbal arguments are really just as convincing as all the mathematics, and their language makes clear the strong connection with Zahavi's arguments. This shows that the models given in this paper is really are models of Zahavi's handicap principle".

The field has progressed much since and many more verifications to the handicap principle pour in every year. Mostly notably, studies using the peacock model system itself by Marion Petrie and her group have provided support to the handicap principle. These are studies that could have easily be done in India, as lamented by Prof. Raghavendra Gadagkar in his excellent review on this topic published in 2003 [9].

In my opinion, scientific progress should be measured by the quantum changes in thought processes. Generators of ideas should be encouraged to discuss their ideas freely without the hesitation of outright rejection and dismissal, on the grounds of not building quantitative models, especially when empirical observations in support of the ideas are persuasive. Did Zahavi get perturbed by rejections on grounds of not having quantitative models to back his theories? I hardly think so. On the contrary, I am tempted to think that not having a mathematically verifiable model to peddle his idea of the handicap principle itself acted as a 'handicap' and went on to indicate the 'honest' quality of his theories, which were eventually verified.

Suggested Reading

[1] Tel Aviv University, Department of Zoology http://www.tau.ac.il/lifesci/departments/zoology/members/zahavi/_baks/zahavi.html.0006.c9b9.bak

[2] A Tal, *Pollution in a Promised Land: An Environmental History of Israel*, University of California Press, 2002.

[3] A Zahavi, K D Harris, V Nanjundiah, An Individual-level Selection Model for the Apparent Altruism Exhibited by Cellular Slime Moulds, *Journal of Biosciences*, Vol.43, pp.49–58, 2018.

[4] C R Darwin, *The Descent of Man, and Selection in Relation to Sex*, London: John Murray, Volume 1, 1st edition, 1871.

[5] R A Fisher, The Genetical Theory of Natural Selection, Dover, New York, 1958.

[6] A Zahavi, Mate Selection: A selection for a Handicap, *Journal of Theoretical Biology*, Vol.53, pp.205–214, 1975.

[7] L Samhita, The Handicap Principle, *Resonance*, Vol.15, pp.434–440, 2010.

[8] A Zahavi, A Zahavi, *The Handicap Principle: A Missing Piece of Darwin's Puzzle*, Oxford University Press, New York, 1997.

[9] R Gadagkar, Is the Peacock Merely Beautiful or Also Honest?, *Current Science*, Vol.85, pp.1012–1020, 2003.

[10] A Zahavi, Reliability in Communication Systems and the Evolution of Altruism, In: B Stonehouse, C Perrins, (eds) *Evolutionary Ecology*, Palgrave, London.

Manjari Jain
Assistant Professor
Department of Biological Sciences
IISER, Mohali
Email: manjari@iisermohali.ac.in